

TOLERANCE AND SEXUAL ATTRACTION IN DESPOTIC SOCIETIES: A REPLICATION AND ANALYSIS OF HEMELRIJK (2002)

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ABSTRACT

Most primate societies are characterized by hierarchical dominance structures. Males are usually dominant over females, but in periods of sexual attraction (during the females' period of tumescence) male "tolerance" toward females rises. Hemelrijk (2002) shows in a model that this tolerance is created as a side effect of the rise of female dominance during periods of sexual attraction. This rise, in turn, is the consequence of the more frequent approaches of males toward females during these periods. In Hemelrijk's model, the males gain no benefit from tolerating females, and they only do so at high aggression levels as a kind of "respectful timidity," because some of the females have become dominant over them.

This paper replicates and examines the results of Hemelrijk's study. We have found that some of Hemelrijk's results are highly reliant on aspects of the model that are not well supported by the current primate literature. We analyze the mechanisms underlying her results and suggest data that should be sought from observation logs of real primate colonies that would support or overturn the model.

Keywords: Agent-based modeling, hierarchy, primates, sexual attraction, social system, tolerance

INTRODUCTION

In this paper, we examine the best-established AI model of primate social systems, Hemelrijk's DomWorld (Hemelrijk 1999a,b, 2000, 2002). Hemelrijk models a large amount of primate behavior by using an incredibly simple model of social interactions based on spatial locations. In this paper, we replicate DomWorld, which allows us to examine the mechanisms underlying the system. We pay particular attention to the results from Hemelrijk (2002), the explanation of the increase of male tolerance experienced by females when they are sexually receptive (in tumescence). This particular experiment, situated in a wider model of differences between species in classifications of primate social structures, gives us a great deal of insight into the validity of Hemelrijk's approach.

We begin this paper by describing the primate social data to be explained and then by reviewing Hemelrijk's contributions. We then present our replication and our initial insights into the working of the DomWorld mechanisms. Finally, we discuss the validity of the model and propose specific data to look for that will either support or undermine the DomWorld model.

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BACKGROUND

Most primate species are highly social. They live in structured societies that can be characterized as having more or less steep dominance hierarchies. A steep hierarchy is one in which individuals would never consider violating rank. For example, a lower-ranked individual would not take any food in the presence of a higher-ranked individual. In a more shallow hierarchy, dominant animals show greater tolerance of subordinate behavior, and considerations of rank play less of a role in ordinary action selection. The difference between these social structures have been most studied in macaque societies (see Thierry et al. 2004 for a recent review). Societies characterized by steep hierarchies are often referred to colloquially as *despotic*, while those with the less rigid dominance structures are called *egalitarian*. When a dominant animal allows subordinate animals to take advantage of resources in its presence, the dominant animal is said to be expressing *tolerance*.

Tolerance is considered one of the most basic forms of conflict resolution (de Waal and Luttrell 1989). It might be difficult to see tolerance as an action to be selected, since it seems more like a form of inaction. However, if an agent is very inclined to preserve resources (including its own social rank), then expressing tolerance can require considerable inhibition of strong inclinations. In some species, for example, this is achieved by the apparently deliberate averting of gaze or even moving away from a resource in order to avoid witnessing a desired event, such as allowing a juvenile throwing a tantrum to feed. This shift in visual attention is necessary if witnessing such an event would automatically trigger an emotional/species-typical response that would, in turn, prevent the completion of the feeding.

The structure of a primate society is also correlated with a number of other characteristics (de Waal and Luttrell 1989; Thierry 2000; Hemelrijk 2002). Societies that are more despotic also tend to have more violent or aggressive interactions. On the other hand, there tend to be fewer conflicts in these societies than in egalitarian societies. In egalitarian societies, there are more frequent conflict interactions, but many of these involve no injury or violent dispute. For example, they may involve only hissing or snatching.

In most primate hierarchies, males are usually dominant over females because of their greater size, strength, and aggression. However, during the female sexually attractive period of tumescence, chimpanzee males, for instance, allow females priority in food access (Yerkes 1940). This has been explained as probably being a cognitive strategy — an exchange for copulation — which is adaptive in that it also therefore produces offspring (Goodall 1986; de Waal and Luttrell 1989; Stanford 1996).

Hemelrijk and her colleagues have proposed a cognitively minimalist explanation of this change in behavior. Hemelrijk claims that there is no statistical evidence for such exchanges for food (Hemelrijk et al. 1992), and neither is there any increase in related offspring (Hemelrijk et al. 1999). Hemelrijk (2002) demonstrates a model where such a change in dominance occurs in despotic societies even without any benefit for the males, but as a simple consequence of the higher frequency of dominance interactions between the sexes brought on by the males' attraction to the females.

Hemelrijk claims that in her models, under the condition of high aggression intensities, males show tolerance toward females. Her evidence of tolerance is that, in her model, in times of sexual attraction, females may achieve ranks higher than males, while in other times, they do not.

Females are modelled as initially 50% weaker than males and persistently 20% less aggressive, which explains why such outcomes are improbable in general. However, once an animal achieves a higher rank, its power is assumed (in these models) to also increase.

Hemelrijk explains her findings as a side effect of the higher frequency at which males approach females. Normally, animals tend to avoid invading each other's personal space and triggering a conflict unless they are of a higher rank than the animal they are approaching. However, in times of sexual attraction, Hemelrijk's males ignore rank in approaching females. Further, in Hemelrijk's model, the outcome of a dominance interaction is highly influenced by the extent to which it was unexpected. Thus if a very-low-ranking female happens to win a competition (there is always a small chance of success, with the probability being inversely proportional to the discrepancy in rank), then she will suddenly achieve a much higher rank.

Consequently, the opportunity for a low-ranking female to win an interaction will rise as more males approach her. Thus, she could become more dominant than some of the males, who will nonetheless continue approaching her, consequently likely increasing her rank as they fail in their subsequent dominance disputes. Therefore this "tolerance" is more a "respectful timidity" toward higher-ranking females. The males will approach but not attack simply because the female has a higher rank.

Thus a behavior typically described as complex or even cognitive could, according to Hemelrijk's model, arise without any corresponding cognition. This change could be introduced to the species through a single exogenous factor, such as the availability of food resources, if this leads to an increase in aggression. This higher aggression then leads to a more despotic society in which in the periods of sexual attraction, the dominance of the females rises, as shown in the model and explained above.

Many researchers have expressed skepticism about Hemelrijk's work because of her anti-cognitivist stance. People who work closely with apes feel that it is "obvious" that the animals have some cognitive capacity, or at least that when humans express very similar behavior, they subsequently report having been in a cognitive state.

Because we were curious about Hemelrijk's model and wished to understand it better, and because no version of DomWorld is freely available on line, we replicated Hemelrijk's work. In so doing, we were able to examine the assumptions behind the model and find out what aspects of the model were critical to its success in replicating primate behavior.

METHODS

Hemelrijk's model consists of a small troop of chimpanzees living near each other and occasionally having aggressive interactions, which result in shifts in dominance rank. After the model has run for a while, quantitative descriptions of the agents' relationships are taken, such as the steepness of the dominance ranking hierarchy or the average centrality of an agent within its troop. These measurements are then compared to measurements made of real chimpanzees in natural situations to judge the quality of the model as a hypothesis of their behavior.

The Model World

Our simulation was based on the model described by Hemelrijk (2002). She wrote her version in Object-Pascal and Borland Pascal 7.0. We used NetLogo 2.1, because it, being a purpose-built modeling tool, provides a relatively easy, high-level language for quickly constructing models and visualizing results. The world in which the agents interact is wrapped around on all sides and therefore resembles the geometrical structure of a torus. This is to avoid border effects and enable the agents to move in every direction. As described by Hemelrijk, this space is of a size 200×200 units. It is a continuous space — agents have real-valued locations and can move in any of 360 directions. When an experiment starts, the agents set initially at random locations within a 30×30 parcel of this space. Each agent has a forward vision angle of 120 degrees (that is, it “sees” or attends to agents that are 60 degrees to either side of its direction of forward motion) and a maximum perception range (*MaxView*) of 50 units. Consequently, at the beginning of the simulation, each agent will need to do no more than turn around to see all the other agents in the simulation. The visual limits restrict the amount of things that the agent is likely to attend to at any particular time.

Agent motion and social interaction is determined by a number of additional threshold parameters:

- A near-perception range, *NearView*, of 24 units. Agents feel comfortable as long as they see some other agent within this range. If they do not, but they do see an agent (that is, one is within *MaxView*), then they will go toward that agent.
- A personal space parameter, *PerSpace*, of 2 units. Agents within this range of each other will have a dominance interaction.
- A search angle of 90 degrees. Agents rotate this amount if they can see no one within their *MaxView*.
- A waiting period. After an agent moves around or engages in a dominance interaction, it is assigned a random waiting time before it performs its next action. The waiting period simulates foraging or resting in the wild — constant dominance interactions are not only unnatural but also make the troop so chaotic that spatial measurements of troop coherence and rank have no meaning. The waiting period is abbreviated when the agent observed a dominance interaction within its *NearView*. This is in accordance with observations in real animals, since in primate groups, nearby fights are likely to trigger active behavior in individuals (Galef 1988).

In our experience, the model does not appear overly sensitive to most of the parameter values, although at the same time, none of them can be eliminated and still maintain the action-selection model. However, the mode *is* particularly sensitive to the organization of the waiting period. This is because many dominance interactions would not happen if the relatively subordinate animals were able to avoid the relatively dominant one, but because only one animal tends to be moving at a time, the dominant one can invade the personal space of the subordinate.

In the simulations dealing with the impact of female tumescence on their dominance ranking, there is one additional parameter, *attraction*, which is either *on*, indicating that all the females are tumescent, or *off*, indicating that none of them are.

The Interaction Structure

The interactions in the model are classified into two groups. One class consists of grouping interactions, the other consists of dominance interactions. These two classes resemble the two forces that in nature, on one hand, drive groups apart, and on the other hand, hold them together in order to stabilize them (c.f. Reynolds 1987).

For the grouping interactions, Hemelrijk gives a set of four rules:

1. An agent that observes another agent within its personal space may perform a dominance interaction, depending on its own rank and the rank of the other agent. For such an interaction, first the nearest potential opponent is chosen. After an interaction, the winning agent moves one unit toward its opponent, while the loser turns around 180 degrees, plus or minus an angle drawn randomly from 45 degrees, then moves two units away.
2. If the agent does not detect anyone in its personal space but can see other agents within its NearView, then — in trials without attraction — it moves one unit forward on its present course. In the attraction condition, if VirtualMale can see VirtualFemale, they will change their direction toward the nearest visible VirtualFemales and then move one unit forward.
3. If the agent detects no other agents within NearView, but there are agents within its MaxView range, then it changes direction toward the nearest one and moves one unit toward it.
4. If there are no other agents within MaxView, the agent turns in a search angle of 90 degrees at random to the right or left.

The dynamics of the simulation are such that, for any agent, there will always be at least one agent still in MaxView in some direction. Occasionally the troop splits, but the agents always reunite shortly. Given the rate of motion of the troop, the maximum duration of the waiting period, and the large difference between MaxView and NearView, no single individual can become “lost” from the troop.

In nature, dominance interactions between primates are characterized by the competition for resources, such as food or potential mates. In order to gain stable access to such resources, the different individuals within a group try to establish a rank in hierarchy that is as high as possible. This is achieved by constant interaction, which Hemelrijk calls in her paper a “long-term ‘power’ struggle.” In the model, there are no resources specified, and the only trigger for interactions is spatial distance. The agents start “fighting” when another agent is within their personal distance and the rank of the other is lower or equal to their own rank. The agent “estimates” its chances to win, and if its chances seem good, then it engages in the competition (see following text).

Since the dominance values *within* each sex are equal at the beginning of a simulation, the outcome of every single interaction influences the chances of winning the next one. Such a system is self-reinforcing and has been shown empirically in many animal species (Hemelrijk 2000).

The formula for determining the outcome of a dominance interaction was modeled after Hogeweg (1988) and Hemelrijk (1999b). Each agent has a certain dominance value, which is readjusted after every “fight” the agent gets involved in. We called this value *Dom* according to Hemelrijk’s notation. This variable is correlated both to the agent’s rank and its ability to win an interaction. If one agent finds another agent in its PerSpace, it compares its own *Dom*-value with the *Dom*-value of the other. If its own value is higher or equal to the other, it “estimates” that it has good chances to win and will therefore interact. The outcome of the interaction is calculated with the following formula (from Hemelrijk 2002, page 734):

$$w_i = \begin{cases} 1 & \frac{Dom_i}{Dom_i + Dom_j} > Random(0,1) \\ 0 & else \end{cases}, \quad (1)$$

where $Random(0,1)$ produces a random real value between 0 and 1.

In this calculation, w_i is the value that determines whether agent i has lost or won. Here 1 means victory and 0 means defeat. The relative dominance value is compared with a randomly drawn number between 0 and 1. If it is greater than the drawn number, the agent wins. This means that higher an agent’s rank is relative to its opponent’s, the more likely the agent is to win.

After a dominance interaction, the dominance values of both agents are adjusted according to the outcome by using roughly the same information:

$$\begin{aligned} Dom_i &= Dom_i + \left(w_i - \frac{Dom_i}{Dom_i + Dom_j} \right) * StepDom, \\ Dom_j &= Dom_j + \left(w_i - \frac{Dom_i}{Dom_i + Dom_j} \right) * StepDom. \end{aligned} \quad (2)$$

The only exception to the above equations is that the lowest possible *Dom*-value is set to 0.01 in order to keep the *Dom*-values positive.

Hemelrijk calls this system for determining dominance values a *damped positive feedback system*, since, in the case of winning, the dominance value of the higher-ranking agent goes up only slightly, but if the lower-ranked agent wins, its dominance value undergoes a great change. This is intended to reflect the fact that it is very unlikely for a low-ranking individual to win an interaction with a high-ranking one. Thus ranking is not changed much by an expected outcome, but it changes greatly for an unexpected one.

The amount of rank shift is also affected by another value: *StepDom*. This value Hemelrijk uses to represent the intensity of the “aggression” (or violence) of the interaction, which she hypothesises also correlates to the impact the interaction has on ranking. She uses a high *StepDom* value to represent the level of aggression in despotic species, and a low *StepDom* value to represent the level in egalitarian ones. Values for *StepDom* can vary from 0 to 1 but are held constant within any give simulation, since they are considered to be determined by species. Although Hemelrijk calls this value “aggression,” note that it has no direct impact on the probability or outcome of an interaction (see Equation 1). Rather, its impact is only indirect through its long-term impact on the dominance values, which do determine both whether and how well an agent fights.

Another important element for correlating Hemelrijk’s models to the real world is understanding her *coefficient of variation of dominance values*. This coefficient indicates the average variation between dominance ranks of the individuals in the troop. Hemelrijk interprets this coefficient as an indication of how despotic or egalitarian a society is. Her hypothesis is essentially that there isn’t a qualitative difference in how monkeys in an egalitarian society treat their superiors versus how those in a despotic one do, but rather that every agent will show an equal amount of respect for a troop mate with twice its dominance value. Thus Hemelrijk represents a despotic society as one with an unambiguously “steep” dominance hierarchy (with a great difference in rank between individuals) and represents an egalitarian one as having relatively ambiguous rankings.

Experimental Setup

For our attempted replications, we used the parameter settings Hemelrijk uses in several studies (Hemelrijk 1999a, 2000). We used eight agents in a troop, four of each sex ($N = 8$). As explained earlier, each agent had an personal space of 2 (*PerSpace* = 2), a vision angle of 120 degrees, a maximum perception range of 50 units (*MaxView* = 50), and near-perception range of 24 units (*NearView* = 24). The search angle was 90 degrees, the fleeing distance was 2 units (*fleeD* = 2), the fleeing angle was 45 degrees at a random direction away from the opponent, and the chasing distance was 1 unit (*chased* = 1) in the direction of the opponent.

To resemble the difference in physical strength between males and females, both sexes started out with different winning or loosing tendencies; that is, the *DomValues* of females were half that of males (*virtual females* = 8, *virtual males* = 16). Also, females have only 80% of the aggression intensity (*StepDom*) of males. The experiment was conducted under four different conditions. We used two level of aggression to correlate with the two types of social interactions witnessed in different primate species. In the high level, the *StepDom* value of males was 1 and that of females 0.8. In the low aggression level, the *StepDom* value of males was 0.1 and that of females 0.08. These two aggression conditions were each run under two conditions of *sexual attraction* (either turned on or off) 10 times each, resulting in a total number of 40 runs. Each run was 42,800 time units long.

RESULTS

Our results match Hemelrijk’s results to the extent that we used the same analysis, which we largely did in order to test the replication. The first figure shows a comparison between the number of interactions performed by virtual females during the different conditions. In the graph,

the total number of aggressive interactions initiated by virtual females is compared for all four different conditions used in the experiment.

In Figure 1, we can see that the number of virtual female dominance interactions increases significantly under conditions with sexual attraction in both intensities of aggression (Mann-Whitney, $N = 10$, $U = 0$, $p < 0.001$, two-tailed, Mann-Whitney, $N = 10$, $U = 0$, $p < 0.001$, two-tailed). That means females are involved in considerably more interactions when they are attractive. The aggression level amplifies the result, even though this effect for the aggression is rather weak (Mann-Whitney U-Test, $N = 10$, $U = 24$, $p < 0.049$, two-tailed).

Figure 2 shows the dominance of virtual females as the sum of the number of males ranked below each female at different times in different conditions. We can see that, as reported in Hemelrijk, female dominance under conditions with a high aggression level increases over time but stays constant under conditions with a low aggression level.

Figure 3 is the classic Hemelrijk result. It shows the distribution of the coefficient of variation of dominance values for both sexes (see discussion in previous section). If aggression is high, there will be a steeper hierarchy (i.e., the difference between rank values will be larger). This is true both within and between sexes. Attraction amplifies this result, despite the fact that some females may outrank some males under this condition.

Figure 4 shows the change of dominance values for both sexes under conditions with high and with low levels of aggression. With high aggression, a constant change in the dominance structure is noticeable as greater and greater differentiation/steepness in the hierarchy. With low aggression, there is only a very small change in the dominance values. This creates a very stable hierarchy where the females never gain a higher positions in the group.

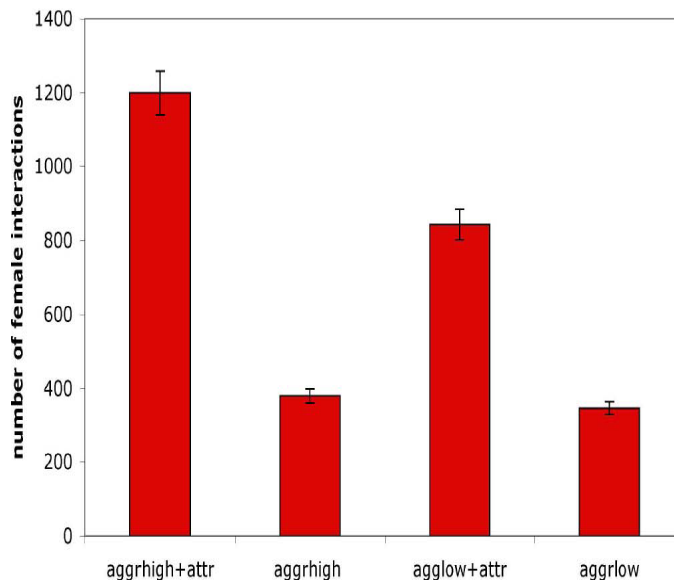


FIGURE 1 Total number of female interactions under different conditions (*aggrhigh+attr* = high aggression + attraction; *aggrhigh* = aggression high + no attraction; *agglow+attr* = aggression low + attraction; *agglow* = aggression low + no attraction.)

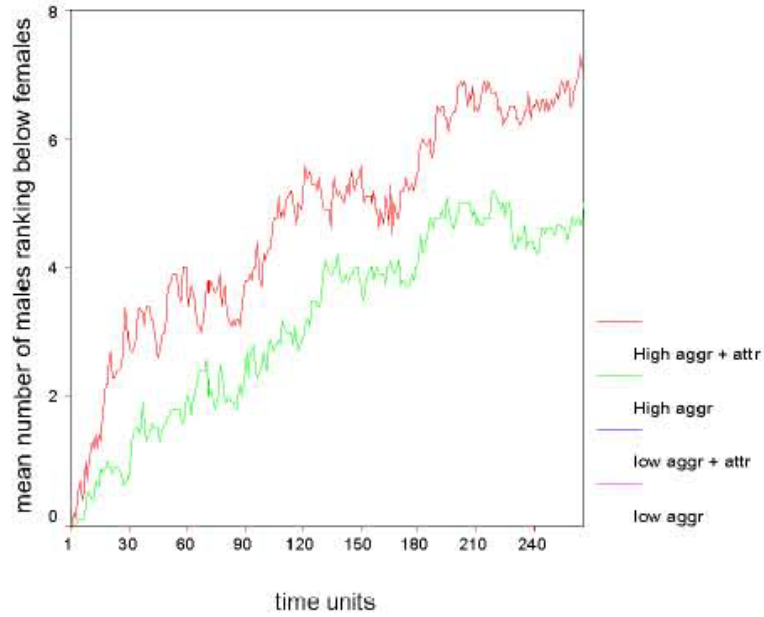


FIGURE 2 Dominance of virtual females as the sum of the number of males ranked below each female at different times under different conditions

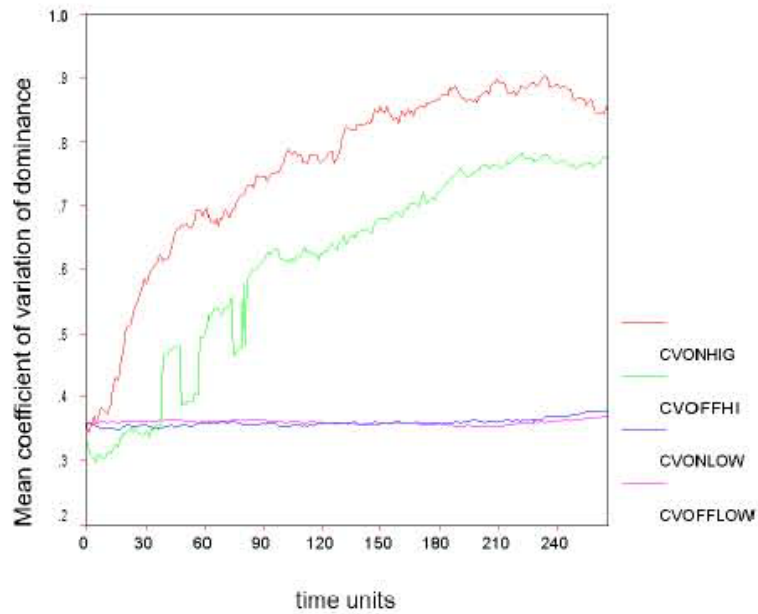
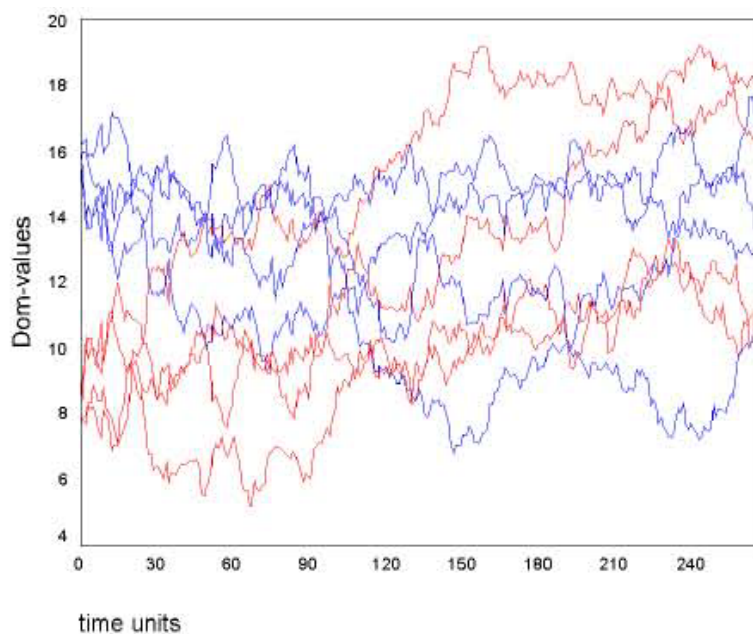
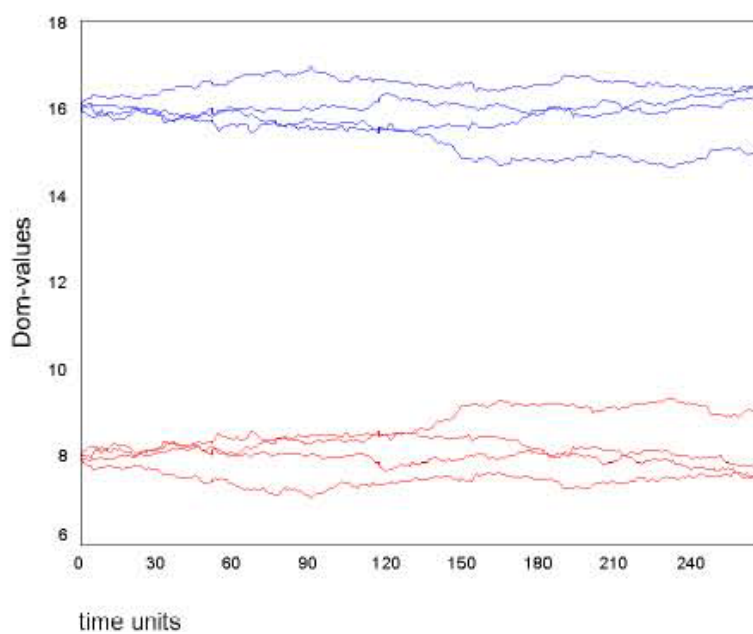


FIGURE 3 Distribution of the coefficient of variation of dominance values under different conditions for both sexes



(a) High level of aggression



(b) Low level of aggression

FIGURE 4 Distribution of dominance values at a high and low level of aggression (Under both conditions, the males start off initially higher than the females.)

The conclusion of these results is that only in groups with a high level of aggression are females able to gain higher positions in the social hierarchy. Attraction amplifies this effect but plays a secondary role.

DISCUSSION

Our results show the same structure as the results in the original study (Hemelrijk 2002, Figure 3A on page 739 and Figures 4A, B, and C on page 741) and can therefore be seen as a replication. In general, the diversity of different dominance values between individuals increases if there is a high aggression level existing within the population. Under conditions with low aggression levels, this effect does not appear, even though the results in this model show that the increase in interactions between virtual females and virtual males depends not on the increased level of aggression but on the existence of female attraction. In this first result, we can see that the level of aggression has no (or, at best, only very little) influence on the number of interactions between the individuals, yet under both conditions, with female attraction, the increase in interactions is significant.

The most interesting effect is the change in dominance values toward more dominant females and, as a possible consequence, a change in group structure. This connection between higher interaction frequency and the dominance value change Hemelrijk claims in her article (see page 742) could be a simple explanation for the observed natural phenomenon of male tolerance toward females in their period of sexual attractiveness. Given our understanding of Hemelrijk's model derived from our replication, we will now examine these claims more closely.

One of the strengths of agent-based modeling (ABM) is its ability to demonstrate whether theories of the origin of behavior can be explained by a given model of how an agent selects its actions. In particular, as with the rest of science, there is an emphasis in ABM on looking for the simplest possible explanation that fits the data. We look for the origins of complex behavioral patterns on a social level as emergent from simple behavior in the individual.

We need to realize, however, that this is not only a case of following the principle of parsimony for reasons of the philosophy of science, it may also be a case of looking for our keys under the light of the street lamp rather than over in the dark where we lost them. Complex individual behavior is difficult to program, takes a long time to execute in simulation, and then is difficult to analyze. So we may have a strong bias toward looking for overly simple solutions. Thus, while on one hand, we need to be open-minded and sure to understand correlations where we find them, on the other hand, we cannot allow our biases to blind us to a situation where data may not fit the predictions of our model. Guarding against this bias is just as important as guarding against its opposite — the overly cognitive explanations.

The Hemelrijk model we have replicated seems to be a good analogue system for macaque behavior. Her DomWorld model shows that apparently complex behaviors in primate societies (like “male tolerance” or “female assertiveness”) can be created in computer-generated primate societies with only a few simple assumptions about individual behaviors. The effect of female dominance appears, for example, under conditions with high aggression and is consolidated by a high level of attractiveness in the females. Hemelrijk notes the difference between this and the classical explanations for this phenomenon, which propose exchanges

involving food for sexual opportunities (Goodall 1986). Hemelrijk's model does not include any food or sex yet still leads to analogous results.

Now that we have a working model, we can try to understand exactly where and how these phenomena “emerge.” We can now analyze what the critical factors of the model are and look for biological correlates that would either prove or disprove the model.

The effect of the model is based on two major assumptions:

1. The self-reinforcing effect of domination and
2. The fact that females attract males in their time of tumescence, but that males are not attractive to females.

The first assumption relates to the fact that the dominance value DOM of an individual i (operationalized as the ability to win a fight) increases with a victory and decreases with a defeat. Although this self-reinforcement is a well-known phenomenon that has been studied extensively in laboratory animals such as mice, we are somewhat skeptical of the exact extent to which this model depends on these factors. In Hemelrijk's model, the strength of the effect is determined by the dominance ranking of the opponent, the level of aggression (i.e., the step-value assigned to this species), and chance. The result of a fight is calculated with Equation 1, repeated here:

$$w_i = \begin{cases} 1 - \frac{Dom_i}{Dom_i + Dom_j} > Random(0,1) \\ 0 \text{ else} \end{cases} . \quad (3)$$

Again as a reminder, the dominance level after a fight is calculated with Equation 2:

$$Dom_i = Dom_i + \left(w_i - \frac{Dom_i}{Dom_i + Dom_j} \right) * StepDom ,$$

$$Dom_j = Dom_j + \left(w_i - \frac{Dom_i}{Dom_i + Dom_j} \right) * StepDom .$$

As we emphasised earlier, Hemelrijk has defined the factor $StepDom$ to mean aggression. An individual therefore increases its ability to win a fight (its dominance) most if it wins against an individual with a preferably much higher dominance level and if the aggression level in the group is high.

Aggression is therefore the crucial value that decides within the system how far an individual can go up or fall down in the hierarchy as the result of a single fight. This is largely the basis of the reinforcement effect of domination. But to what extent does this effect exist in nature? Hemelrijk's text only mentions observations of bumblebees and other computational models as examples (page 743 f). Thinking about it in a intuitive way, it might be plausible that self-confidence about winning a fight increases if one wins against someone much stronger. Further, we know that even in adult mammals, growth hormones can be triggered by success in

social competitions. Nevertheless, in a real fight, the body's size and strength are at least as important as the psychological status of the individual.

To test the validity of Hemelrijk's model, we need to use the documented history of dominance hierarchies in real animals. We need to look carefully at the relatively rare events in which a lower-ranked animal bested a higher-ranking animal and see what the impact was on the troop's dominance structure before and after. We should look in particular for the following factors:

- If one agent defeats another that vastly outranks it in a dominance interaction, do the two agents immediately change ranks within the troop? In other words, is an unexpected outcome from a fight likely to have a very significant effect? If this is true, it would validate the use of relative dominance values in Equation 2.
- In comparing across species, does it take fewer interactions to advance rank in a despotic species? If this is true, then it would justify the use of StepDom in Equation 2.
- Within species, if a fight is more violent (e.g., if blood is drawn compared to mild beating, or if there is mild beating compared to a nonphysical interaction), does it have more impact on dominance hierarchy? If this is so, then it makes sense to refer to StepDom as "aggression," and it would further validate its use in Equation 2.
- Are females more likely to engage in fights when they are tumescent? If not, then this model cannot account for their increased dominance.
- Do females only become dominant during their tumescence in despotic species? Given that in Hemelrijk's model, the prime indication of increased dominance for females is the males' increased tolerance of them, discriminating an increase of rank in an egalitarian species may be difficult, since these species are by definition tolerant toward all group members. But it is a prediction of the model.
- Is it true that when an animal in an egalitarian species is *clearly* outranked by another animal, those two animals' interactions will be similar to two more nearly ranked animals in a less egalitarian species? Or *is* there a qualitative difference in how different species behave with respect to dominance hierarchies? The answer to this question will serve to validate whether the steepness of the dominance hierarchy is a good representation of despotism/egalitarianism.

Of course, this is complicated by the fact that establishing a dominance hierarchy is never easy. It's not clear that every animal will agree on the current hierarchy; indeed, some animals will behave differently with respect to others depending on what other animals are present (Harcourt 1992). However, many groups work diligently to attempt to establish these sorts of records, so we can hope to test these predictions.

We need to also look critically at the second basic assumption: the idea that female primates attract male primates when they are in their fertile days. This is obviously true, but sexual attraction is bidirectional and therefore influences the grouping behavior of females as well. Of course, it is possible that the male attraction is strong enough to overwhelm the data, or even that just putting high male attraction is a good approximation for mutual attraction. However, the question remains as to whether the mechanism exploited by the model — increased conflict leading to a higher probability of an occasional lucky win by the female that immediately catapults her high into the dominance hierarchy — is at all plausible.

6 CONCLUSIONS

We have presented a replication of Hemelrijk (2002) and an analysis of how her model works. We have also presented a critical list of suggestions for testing the validity of the mechanism. We suspect that the rules for determining dominance from the outcome of dominance battles are not sufficiently realistic and cannot fully explain the change in female dominance rank on their own. If we are right, then this model may need additional factors to explain this phenomenon, possibly including a cognitive state sufficient for the traditional theories of reciprocation.

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